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THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

CHAPTER III.

The Specialization of Wings by Reduction.

I. INTRODUCTION.

THE recognition of certain features of the venation of the wings of insects which occur in the more generalized forms of a large proportion of the orders of this class has enabled us to present a hypothetical type to which the wings of all orders may be referred. A detailed discussion of the features of this type has already been given; the figure representing it is repeated here (Fig. 5) in order that it may be easily compared with figures of actual wings. It represents the supposed arrangement of the tracheæ in a wing of the nymph of the primitive winged insect. By omitting the basal part, the figure will also serve to show the number and arrangement of the longitudinal wing-veins of the adult.

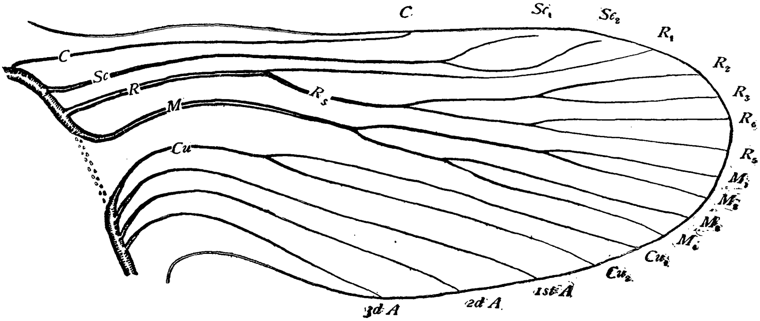

FIG. 5.— Hypothetical type.

It will be seen at a glance that this hypothetical type differs from the great majority of living insects in the possession of a larger number of wing-veins than is characteristic of them; it also differs, and in a more striking degree, from most of the insects of the Linnean order Neuroptera in having a much smaller number of wing-veins than is possessed by them.

These differences indicate two different methods of specialization by which this primitive type has been modified: the one, specialization by reduction; the other, specialization by addition.

We postpone any farther reference to the latter method of specialization and confine our attention in this place to a study of some of those forms in which a tendency to modify the primitive type by a reduction in the number of wing-veins is evident.

A reduction in the number of wing-veins takes place in two ways: first, by atrophy of veins; second, by the coalescence of two or more adjacent veins.

The first method is illustrated in most of the orders where a reduction in the number of wing-veins has taken place by the atrophy, more or less complete, of one or more of the anal veins; this is correlated with a reduction in the extent of the anal area. This method is also illustrated in certain cases where there is no apparent reduction of the area of the wing from which the vein has disappeared. The most familiar illustrations of this occur in the Lepidoptera. In this order, as is well known, the main stem of the media disappears in many families; and in the geometrid moths of the family Eunomidæ, the second branch of this vein is also lost.

The second method of reduction — that is, by coalescence — takes place in all of the orders in which the number of wing-veins is less than in the typical wing. This also takes place in two ways: first, the point at which two veins separate occurs nearer and nearer the margin of the wing, until finally, when the margin is reached, a single vein remains where there were two before; second, the tips of two veins may approach each other on the margin of the wing until they unite, and then the coalescence proceeds towards the base of the wing. The former is a coalescence extending outward; the latter, a coalescence extending inward. Examples of the former are common in all of the orders discussed in this chapter; illustrations of the latter are most easily observed in the Diptera.

The typical arrangement of the wing-veins is often modified, also, by an anastomosis of two veins; that is, two veins will come together at some point more or less remote from their extremities and merge into one for a greater or less distance, while their extremities remain separate. This is illustrated in Nemoura (Fig. 8), where veins Sc_2 and R_1 anastomose.

In the preceding chapter we suggested a nomenclature of the principal wing-veins and of their chief branches, which is applicable to all of the orders of winged insects. At that time nothing was said regarding the cross-veins; for it seems hardly practicable to propose a nomenclature of these based on homologies which shall have an equally general application. This arises from the fact that in those orders where the number of wing-veins is greatly increased, the primitive cross-veins, if such exist, are in most cases indistinguishable from those that have been developed secondarily.

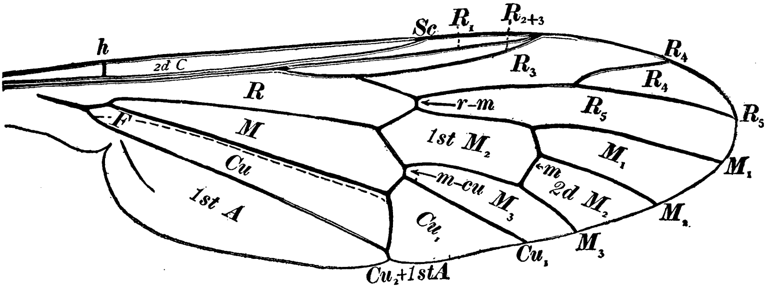

FIG. 6. — Wing of a Leptid, showing cross-veins and cells.

But when we examine the wings of those orders in which the tendency is towards a reduction in the number of wing-veins, we find that there are a few cross-veins which are so constant in their position and which occur in so many widely separated groups that they are evidently homologous. As the number of these is small, we propose to designate them by names, as follows:

The humeral cross-vein. This is a single cross-vein extending from the subcosta to the costa near the humeral angle of the wing (Fig. 6, *h*). This is the most constant of all of the cross-veins.

The radio-medial cross-vein. This is a cross-vein extending from radius to media, usually near the center of the wing, and is designated by the abbreviation *r–m*. When in its typical position, this cross-vein extends from R_{4+5} to M_{1+2}; this results in one end being opposite cell R_3 and the other end opposite cell 1st M_2. The cells are defined a little later.

The medio-cubital cross-vein. This is a cross-vein extending from media to cubitus, usually near the center of the wing. It is designated by the abbreviation *m–cu*. When in its typical position this cross-vein extends from a point near the base of M_{3+4} to a point near the base of Cu_1.

The medial cross-vein. This is a cross-vein extending from media-two (M_2) to media-three (M_3); this is designated by the abbreviation *m*. The presence or absence of this cross-vein is often a character of considerable taxonomic importance.

The arculus. In many insects there is what appears to be a cross-vein extending from radius to cubitus near the base of the wing. This has been termed the arculus by writers on the Odonata, and we propose to extend the use of the term to all orders in which there is a similar arrangement of the veins in this part of the wing. The arculus is designated by the abbreviation *ar*. Usually when the arculus is present the media appears to arise from it. The fact is, the arculus is compound, being composed of a section of the media and a cross-vein. The structure of this part can be clearly seen in the Odonata (Fig. 7).

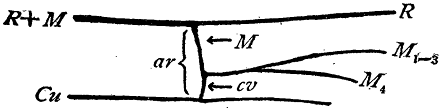

FIG. 7. — The arculus, diagrammatic.

In descriptions of wings it is often desirable to refer to one or more of the cells. It is necessary, therefore, to have a nomenclature of the cells of the wing, as well as of the wing-veins. Certain of the cells have received special names; but as no effort has been made by those proposing them to trace the homologies of the cells beyond the limits of a single order, the names proposed are not available for our present purposes. A single example will serve to illustrate this. We find the term *discal cell* used in descriptions of Lepidoptera, Diptera, Trichoptera, and Corrodentia (Psocidæ), but in no two of these orders is it applied to the same cell.

Having named the wing-veins, the simplest possible method of designating the cells of the wing is to apply to each the abbreviation of the name of the vein that forms its cephalic (front) margin. It should be borne in mind, however, that by modifications of the typical arrangement of the wing-veins, a vein that normally forms the cephalic margin of a cell may apparently bear a very different relation to it; and this must be taken into account if we are to apply the same term to homologous cells throughout the insect series.

The cells of the wing fall naturally into two groups: first, those on the basal part of the wing; and second, those nearer the distal end of the wing. The former are bounded by the principal veins; the latter, by the branches of the forked veins; a corresponding distinction is made in designating the cells. Thus the cell lying behind the main stem of radius and on the basal part of the wing is designated as cell R; while the cell lying behind radius-one is designated as cell R_1.

It should be remembered that the coalescence of two veins results in the obliteration of the cell that was between them. Thus when veins R_2 and R_3 coalesce, as in Leptis (Fig. 6), the cell lying behind vein R_{2+3} is cell R_3 and not cell R_{2+3}, cell R_2 having been obliterated.

When one of these principal cells is divided into two or more parts by one or more cross-veins, the parts may be numbered, beginning with the proximal one. Thus in Leptis (Fig. 6), cell M_2 is divided by the medial cross-vein into two parts, which are designated as 1st M_2 and 2d M_2, respectively.

The application of this system of naming the cells of the wing is an easy matter in those orders where the wings have few veins; but in those orders where many secondary veins are developed it is more difficult of application. In the latter case we have to do with *areas* of the wing rather than with separate cells. Thus, for example, it will be shown later that in certain Neuroptera the area R_2 is divided by several longitudinal veins, which are connected by many cross-veins, the area R_2 (which is strictly homologous with cell R_2) being composed of a large number of secondary cells.

The wings of comparatively few insects present a flat surface; in most cases we find that the membrane is thrown into a series of folds or corrugations. This corrugating of the wing in some cases adds greatly to its strength. This is well shown by the wings of dragon flies; and in most orders the costal margin of the wing is strengthened by a fold between costa and radius, the *subcostal fold.* In other cases, the corrugations are the result of a folding of the wing when not in use; this is well shown in the anal area when this part is broadly expanded.

It rarely happens that there is occasion to refer to individual members of either of these classes of folds, except, perhaps, to the one that has just been designated as the subcostal fold. But there are three other furrows which it is necessary to designate, as we shall have frequent occasion to refer to them. These we term the anal furrow, the median furrow, and the nodal furrow, respectively. They may be defined as follows:

The anal furrow. This is a longitudinal furrow which is usually between the cubitus and the first anal vein (Fig. 6, *F*). It has been referred to by many writers, but the variableness of its position has not been pointed out.

The median furrow. This is a longitudinal furrow which is usually between radius and media. It is well marked in many of the Hemiptera, where it separates the embolium from the remainder of the corium; and in the Hymenoptera its course is marked by a series of weak spots (bullæ) in certain veins.

The nodal furrow. This is a transverse suture beginning at a point in the costal margin of the wing, corresponding to the nodus of the Odonata and extending towards the inner margin of the wing. It crosses a varying number of veins in different orders of insects.

The furrows of the wing are in no sense homologous or even analogous to veins. More than this, as will be shown repeatedly, the relative positions of the furrows and of the wing-veins are not constant; for it frequently happens that the course of a vein has been so modified that it crosses the line of a furrow and the relative positions of the two are thus reversed. If this fact had been understood by Adolph we would have been spared his misleading theory of alternating concave and convex veins.[1]

II. THE VENATION OF THE WINGS OF CERTAIN PLECOPTERA.

If we leave out of consideration the anal area, that portion of the wing traversed by the anal veins, we will find that in nearly every case each order of insects is characterized by either a reduction or a multiplication of the wing-veins; in certain orders the tendency is in one direction, while in others it is in the opposite. But either of these tendencies may be correlated with a similar tendency in the anal area or with the opposite one. In this chapter we purpose to point out the ways in which the primitive type of wing venation has been modified in representatives of several of the orders where a reduction in the number of wing-veins in the preanal area has taken place.

In the order Plecoptera, or stone flies, we find that, although in most genera the anal area of the hind wings has been expanded and the number of anal veins increased, in the preanal areas of both wings the number of wing-veins has been increased in certain genera and reduced in others; and we cannot say that either of these tendencies has yet attained the ascendency within this order.

This fact, taken in connection with the generalized condition of the basal attachments of the tracheæ of the wings, already pointed out, leads us to believe that the Plecoptera as a whole depart less widely from the primitive winged insect than do the living representatives of any other order.

In this place, we have to do only with those Plecoptera in which a reduction in the number of wing-veins in the preanal area of the wing has taken place. Of these, the genera Nemoura and Tæniopteryx are taken as examples. And we use, for the purposes of this study, wings of nymphs taken at a stage when the forming wing-veins appear as light-colored bands and the tracheæ, about which they are formed, as dark lines.

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[1] G. Ernst Adolph, Ueber Insectenflügel. *Nova Acta der ksl. Leop.-Carol.-Deutschen Akademie der Naturforscher.*, Bd. xli, pp. 215–251. 1879.

In the nymph of Nemoura (Fig. 8) we have not observed a costal trachea. The subcosta is forked in the typical manner, and vein Sc_2 anastomoses with vein R_1. The radius is reduced, the radial sector being only two-branched; it is probable that this reduction came about by the coalescence outward of vein R_2 with R_3 and of vein R_4 with R_5. The media is reduced in a similar way. The cubitus is typical, but in the fore wing several cross-veins have been developed between its branches, and also between it and the media; the strengthening of this region of the fore wing is quite characteristic of the Plecoptera. The anal veins are typical in the fore wing, but in the hind wing the second and third anal veins are each forked.[1]

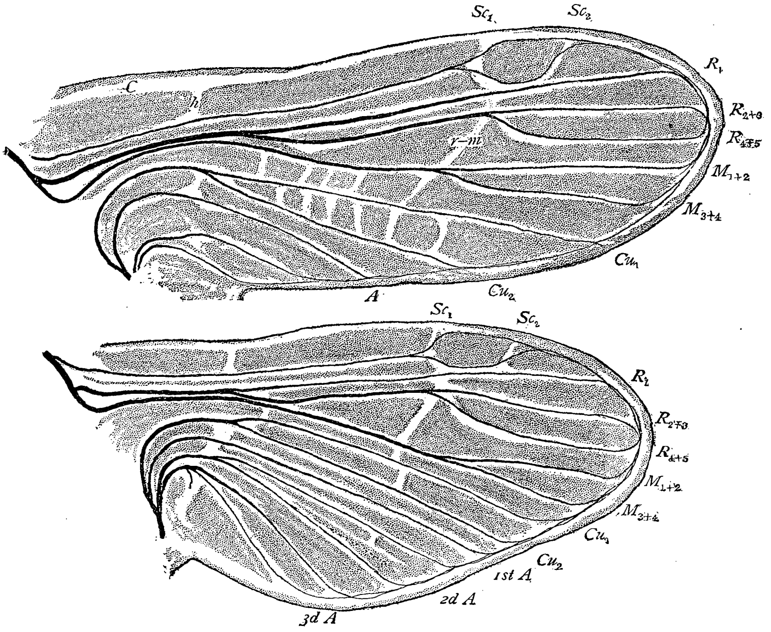

FIG. 8.—Wings of Nemoura, nymph.

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[1] There is a striking similarity between the anal areas of the Plecoptera and the Orthoptera; throughout both these orders the first anal vein remains simple in both wings, but the second and third anal veins are forked when this part of the wing is expanded.

The wings of a nymph of Tæniopteryx (Fig. 9) show a slightly different modification of the type. The costal trachea is well preserved. The subcosta is typical. The radial sector is reduced even more than in Nemoura, the coalescence of veins R_{2+3} and R_{4+5} having extended to near the margin of the wing; the carrying of this process a little farther would reduce the radial sector to an unbranched condition, which is what has happened in some species of this genus (Fig. 10). The media is three-branched in the fore wing and two-branched in the hind wing, but in the hind wing vein M_{3+4} coalesces with vein Cu_1. The

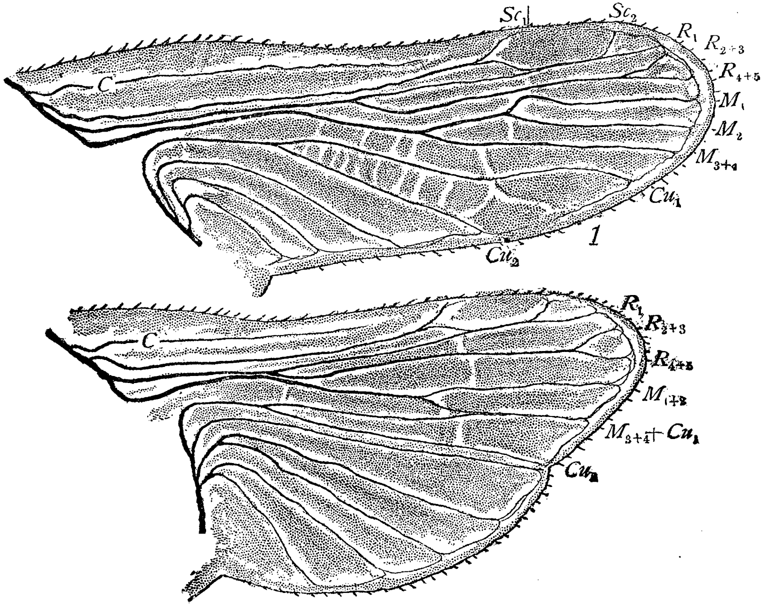

Fig. 9. — Wings of Tæniopteryx, nymph.

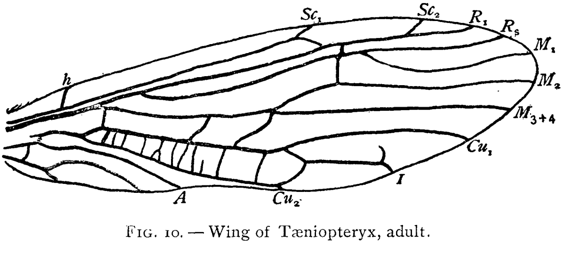

Fig. 10. — Wing of Tæniopteryx, adult.

cubital trachea is typical in both wings, and the anal veins are quite similar to those of Nemoura.

There are two points of especial interest in the fore wing of this insect, both showing the importance of ontogenetic study in determining the homologies of wing-veins.

First, it is evident that, correlated with the great reduction of the radial sector, vein M_1 of the fore wing, which remains distinct from vein M_2 in this genus, has come to perform the function that is performed by vein R_{4+5} in Nemoura; and, as a result, it has assumed a similar position. So great is the similarity that one who studied only the wings of the adult Tæniopteryx would be certain to mistake vein M_1 for a branch of the radial sector. A glance at Fig. 10, which represents the fore wing of the adult of another species of this genus, will make this more evident. If the object in view were merely to number the wing-veins, it may be that a mistake of this kind would not be serious; but when the object is to determine the relationships of allied forms, such a mistake would surely lead one astray.

The second point illustrates specialization by addition, and it is anticipating somewhat to allude to it here. It will be observed that in Fig. 10 a vein which ends in the margin of the wing midway between veins Cu_1 and Cu_2 is labeled 1. This is what we shall define later as the first accessory cubital vein. A reference to Fig. 9 will show that, although this vein has the same appearance as other longitudinal veins in the adult, it is not preceded by a trachea in the nymph, but, like the cross-veins, is formed secondarily. This is an illustration of the beginning of a process which is carried to a great extent in those insects that have wings with many wing-veins, and which will be described in more detail later.

It will be seen from these two illustrations that a study of the ontogeny of the wings opens a fruitful field to one engaged in a study of the genetic relationships of winged insects.

III. THE VENATION OF THE WINGS OF PSOCUS.

The determining of the homologies of the wing-veins in Psocus and allied genera is a problem that has sorely puzzled all who have worked upon it; and it has remained till now unsolved, although it has been attacked by such writers as Hagen, McLachlan, and Kolbe.

But when it is approached by the ontogenetic method the difficulties vanish, and it is hardly necessary to do more for its solution than to refer to the accompanying figures representing three stages in the development of the fore wing of *Psocus venosus*. When one understands this wing, the working out of the homologies in the hind wing, which is more reduced, and in the wings of other genera is a comparatively simple matter.

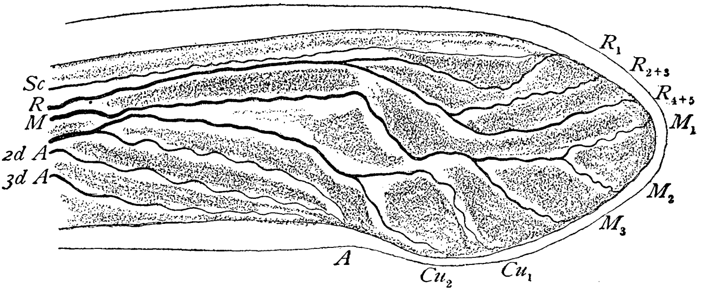

FIG. 11. — Psocus, fore wing of a nymph.

Fig. 11 represents the wing of a nymph which was not yet full grown. The lettering of the figure indicates the homologies of the tracheæ. The formation of the wing-veins has begun, but in most cases the outlines of these are vague. It will be observed that the wing is much smaller than the enveloping sheath.

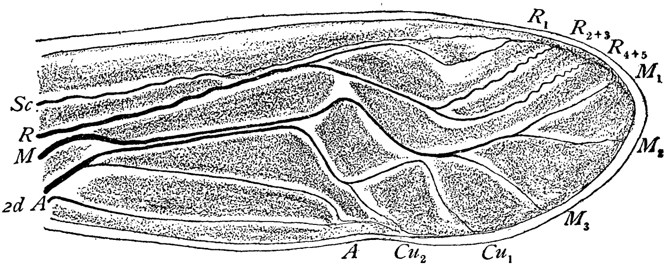

FIG. 12. — Psocus, fore wing of a full-grown nymph.

Fig. 12 represents the wing of a full-grown nymph. Here the forming veins are much more definite in outline, and there is no difficulty in tracing the venation of the adult wing. The costal trachea is preserved for only a short distance; the subcostal trachea extends far beyond the end of the forming vein; and for a considerable part of its course is within the light band that is to form the radius; the radial sector has been reduced to two branches; and only three branches of the media remain. The most striking features of this wing are the coalescence of media and cubitus, which is shown by the two tracheæ being closely parallel for a considerable distance within a single vein, and the zigzag course of media, which is easily determined by following the course of the medial trachea. Neither of these features is so well marked in the less mature wing. The first anal vein coalesces with cubitus at the base. The second anal vein has moved nearer to the margin of the wing. And the third anal trachea is no longer visible.

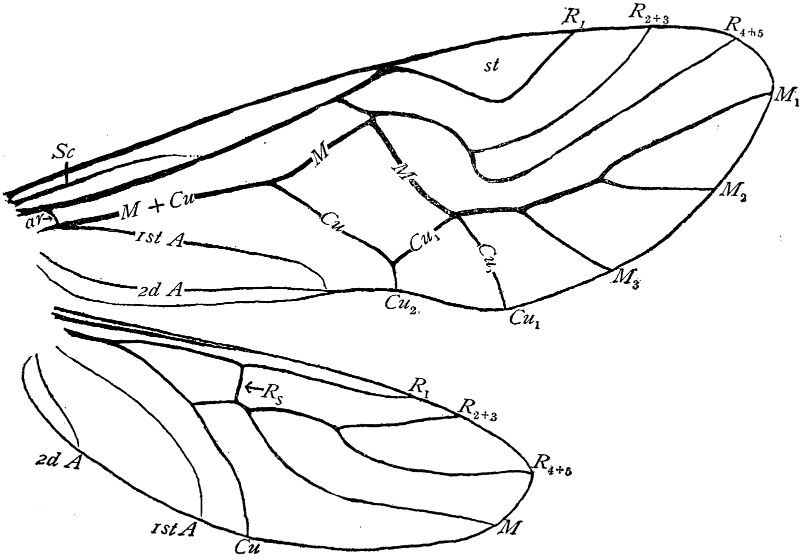

FIG. 13. — Psocus, wings of an adult.

The wings of the adult are represented by Fig. 13. A remarkable feature of these wings is that, although they are braced in every direction, there is not a single cross-vein present, except an arculus which is formed of the base of the media; the bracing is accomplished by the zigzag courses of the principal veins. This, however, is not true of all psocids. In some the bend in the media does not reach the radial sector, and the two are connected by a radio-medial cross-vein.

The margin of the adult wing is tubular throughout, there being what has been termed by writers on the Diptera an ambient vein. The costal and anal portions of this doubtless represent the costa and third anal veins, respectively, although the corresponding tracheæ are apparently lost. The distal portion of this ambient vein was preceded by the anastomosing tips of all of the veins, as is shown in the figures of the nymph wings. In the fore wing the tip of the subcosta coalesces with the radius; in the hind wing it coalesces with the costa. In the fore wing a large stigma is developed in an angle of vein R_1; and in both wings the anal furrow coincides with the first anal vein.

IV. THE VENATION OF THE WINGS OF A CICADA.

A study of the wings of Hemiptera reveals remarkable departures from the primitive type of wing venation. So great are these that, at first, one sees very little in common between the wings of a bug and those of insects of any other order. We were filled with delight, therefore, when we found within this order, preserved almost unchanged, what we had come to regard, from a study of other orders, as the primitive type of wing venation.

The conservative Hemiptera that retain most perfectly the fashions of ancient times, so far at least as concerns the venation of the wings, are the cicadas. But the slightness of the changes that have taken place is not obvious if one studies only the wings of the adult; for in this stage there is a massing of several veins along the costal margin of the wing, and the cross-veins have the same appearance as the branches of the primary veins.

In the wings of a young nymph, on the other hand, the tracheæ that precede the primary veins are not massed as they are later, and in the older nymph where the forming veins appear as pale bands the cross-veins contain no tracheæ.

In the wing of a nearly mature nymph (Fig. 14) the costal trachea extends nearly to the apex of the wing. The subcostal trachea is also prominent, but it is not forked. The radius is reduced to a three-branched condition. The media is typical. So, too, is the cubitus. The first anal trachea coalesces with the cubital trachea for a considerable distance. The second and third anal tracheæ are also united at the base, and the forming veins appear as pale bands.

The important departures from the primitive type are two: first, the coalescence of the first anal vein with the cubitus. This results in the anal furrow of the adult lying between the first and second anal veins; but these two are closely opposed in the fore wing of the adult, except for a short distance at the base of the wing, so that they appear as a single vein along the line of the furrow. The study of the wings of an adult which was killed at the moment of emergence from the nymph skin, and in which the tracheæ of the wings are distinctly visible within their corresponding wing-veins, has materially aided us in determining the relation of the anal furrow to the adjacent veins. It may be said in this connection that the coalescence of the first anal vein with the cubitus is a common occurrence in several of the orders.

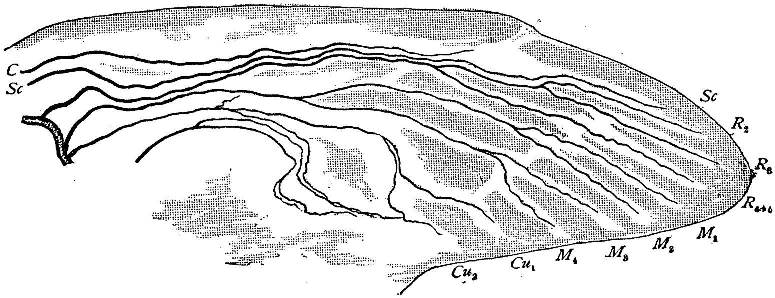

FIG. 14. — Cicada, fore wing, mature nymph.

A more striking departure from the primitive type is the reduction of the radius. For a long time we were unable to decide in what manner this had taken place. The usual mode of reduction of this vein is by the coalescence outward of the two branches of each half of the radial sector, leaving the sector two-branched and the vein as a whole three-branched, as in Nemoura and in Psocus. But in these cases the intermediate branch of the radius arises from the posterior one of the three; in Cicada, on the other hand, the intermediate branch arises from the anterior one of the three (Fig. 14).

It was not till we succeeded in obtaining a very young nymph of Cicada that this question was definitely settled. In the fore wing of this nymph (Fig. 15) the radial trachea is five-branched; and the only departure from the typical mode of branching is that the branch which corresponds to vein *R*1 coalesces for a short distance with the one corresponding to the anterior half of the radial sector.

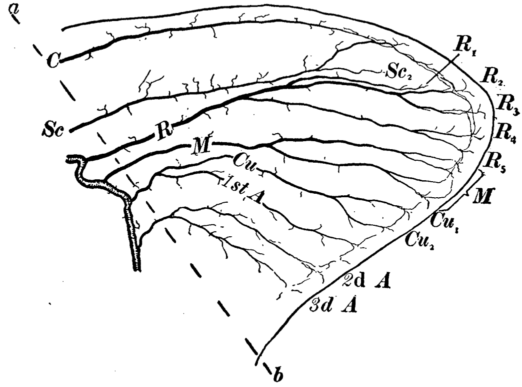

FIG. 15.— Cicada, fore wing, young nymph.

It will be observed that in this part of the wing the subcostal trachea closely approaches the radial. This crowding of the radial trachea by the subcostal is doubtless the explanation of the pushing outward of the point of separation of the trachea *R*1 and of the complete atrophy of this trachea in the later stages of this insect, which results in the non-development of vein *R*1.

We have discussed this matter at some length, not merely to show the close correspondence of the tracheation of the wing of the young nymph to our hypothetical type, but also to point out the course by which has been reached one of the most characteristic features of the venation of the wings of Hemiptera, that is, the complete absence of vein *R*1.

From a study of the two nymph wings figured here, it is an easy matter to trace the homologies of the veins and cells of the fore wing of the adult; these are indicated by the lettering of this part in Fig. 16.[1] The more difficult points are eluci-

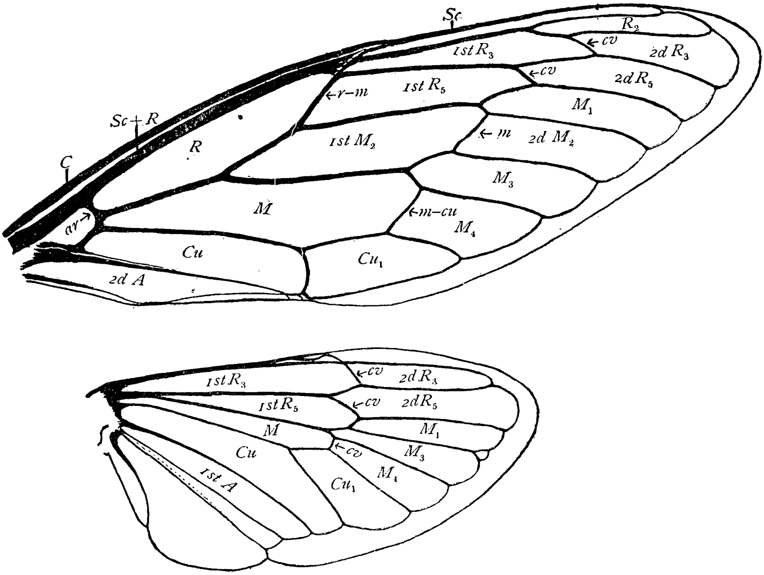

FIG. 16. — Cicada, wings of adult.

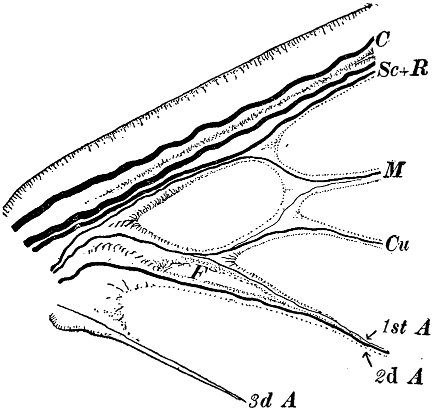

FIG. 17. — Cicada, base of fore wing.

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[1] In those cases where the veins are not numbered, their homologies are indicated by the numbering of the cells behind them.

dated by Fig. 17, which represents the base of the fore wing of the adult, and Fig. 18, which represents the region of the nodal furrow of the same wing. These figures are based on a study of the recently emerged adult, already referred to. We wish to call attention especially to the coalescence of subcosta and radius from the base of the wing to a point near the nodal furrow, as this is a feature which occurs in a large proportion of the families of the Hemiptera.

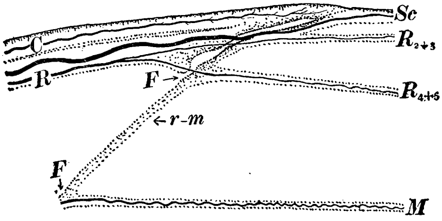

FIG. 18. — Cicada, nodal furrow of the fore wing.

The changes that have taken place in the hind wing of Cicada are much greater than those of the fore wing, and it would be exceedingly difficult to understand them without the aid of ontogenetic study. But a careful comparison of the hind wing of a young nymph (Fig. 19) and the base of the hind wing of the recently emerged adult (Fig. 20) has cleared up the doubtful points.

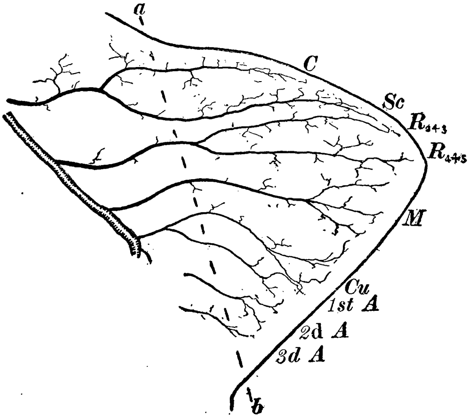

FIG. 19. — Cicada, hind wing, young nymph.

In comparing the wings of nymphs, and especially of young nymphs, with those of the adult, it will be found that the growth of the basal part of the wing proceeds more rapidly at first than does that of the distal portion. This is shown by the fact that the branching of the branched tracheæ occurs much nearer the outer margin of the wing in the nymph than does the branching of the corresponding veins in the adult.

The difference is not so great, however, as appears at first sight, for only a part of what is represented in Fig. 19 corresponds to the wing of the adult. The dotted line *a–b* indicates approximately the line along which the hinge of the wing of the adult is formed. In Fig. 15, the line *a–b* represents the corresponding part in the fore wing.

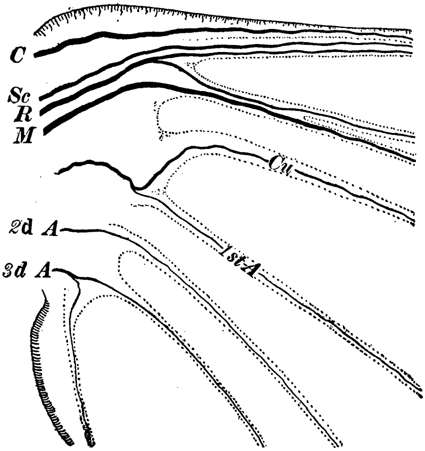

FIG. 20. — Cicada, base of hind wing.

By comparing Figs. 15 and 19 it will be observed that the forking of the radial trachea takes place much nearer the hinge line in the hind wing than it does in the fore wing. Upon this fact depends the most striking difference in the venation of the fore and hind wings of the adult.

In the fore wing we found that subcosta and radius coalesce to a point near the nodal furrow. But in the hind wing it is only the anterior half of what is left of the radius after the loss of vein R_1 that coalesces with the subcosta. The posterior half, vein R_{4+5}, separates from vein R_{2+3} very near the base of the wing, and coalesces with the media for a short distance, after which it traverses the wing as a separate vein. A result of this is that while the 1st cell R_3 of the fore wing lies beyond the nodal furrow, in the hind wing it reaches the base of the wing; and the 1st cell R_5 occupies a similar position. A study of the base of the hind wing of the recently emerged adult (Fig. 20) confirms these conclusions.

Other features of interest in the hind wing are the following: The media is only three-branched as a rule, but in some specimens there is a small remnant of cell M_2. The first and second anal veins are widely separate, and the third anal vein is forked.

In the course of the development of the wing of Cicada there is an excellent illustration of the migration of the base of the medial trachea, which was referred to at the close of Chapter II. In the young nymph of Cicada (Fig. 15) the medial trachea arises from the transverse basal trachea midway between the radial and cubital tracheæ. In the mature nymph (Fig. 14) the base of the medial trachea has reached the cubital trachea.

In tracing the homologies of the tracheæ of the wings, it is very important that this migration of the base of the medial trachea be kept in mind. For while in the more generalized forms where there is no basal transverse trachea (Plecoptera and certain Blattidæ) the medial trachea belongs to the costo-radial group of tracheæ, whenever a basal transverse trachea is present the medial trachea either arises from it or is a member of the cubito-anal group. The ontogeny of Cicada gives conclusive evidence of this migration. In all mature nymphs of Hemiptera that we have examined the migration has taken place, the medial trachea being a member of the cubito-anal group.

V. THE VENATION OF THE WINGS OF HETEROPTERA.

In Cicada we found the most generalized condition of the wings that exists in the hemipterous insects that we have studied, and it is hardly to be expected that a more generalized form will be found among the living representatives of this order. We have now to consider modifications of this type in representatives of the suborder Heteroptera.

In our studies of Heteroptera we have examined nymphs of the following families: Notonectidæ, Nepidæ, Belostomidæ, Reduviidæ, Nabidæ, Capsidæ, and Pentatomidæ. Of these there is no doubt that the most generalized condition of wing venation is found in the family last named, but further studies in other families may reveal a still more primitive type.

Fig. 21 represents the tracheation of the fore wing of a Pentatomid nymph. In this wing the costal trachea is well preserved. The subcostal and radial tracheæ are closely approximate in the basal half of the wing; in the distal half of the wing the subcostal trachea traverses that part of the wing which would be traversed by trachea R_1 were it well developed and in its typical position; but it is reduced to a rudimentary condition. It is evident that a supplanting of R_1 by the subcosta takes place here, as in Cicada. The trachea that precedes the radial sector has its characteristic bend at the base, and is two-branched. The medial trachea is typical, that is, four-branched. The cubital trachea is six-branched; it is evident that a specialization by addition has taken place here. Only a single anal trachea has been preserved.

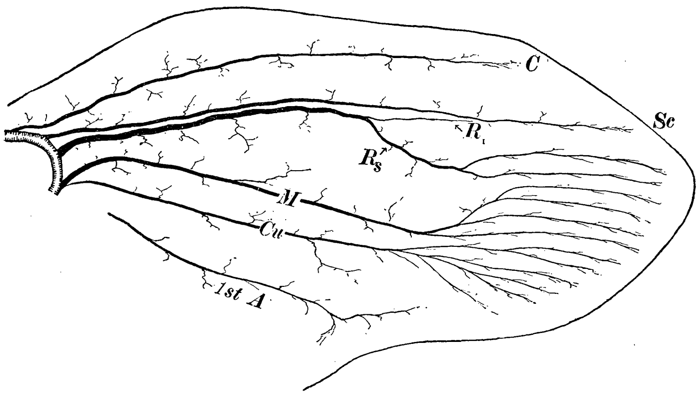

FIG. 21. — A Pentatomid, fore wing, nymph.

The hind wing of the same nymph (Fig. 22) presents a very similar arrangement of tracheæ, except in a greater reduction of the radius.

Unfortunately, we did not rear any adults from nymphs of this species; hence we cannot give a figure of the adult wing of this particular insect. But an examination of many Pentatomids shows that in the thickened portion of the fore wing the tracheæ follow essentially the same course as in the nymph figured here. There are also faint longitudinal veins in the membranous terminal portion of the wing which doubtless correspond with the tips and branches of the principal tracheæ. But at the base of the "membrane," as this terminal portion is designated by writers on the Hemiptera, a hinge line is formed, across which it is rarely possible to trace the tracheæ in dried specimens. The veins of the membrane appear to be connected by cross-veins parallel with this hinge line and close to it, and have but slight connection with the veins of the basal part of the wing except near the end of the anal furrow. We are not able, therefore, with the material at hand, to work out the homologies of the veins of the membrane, and must be content with pointing out at this time the more important features of the thickened portion of the wing.

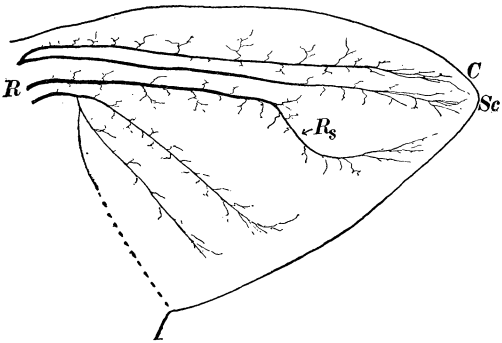

FIG. 22. — A Pentatomid, hind wing, nymph.

In those Pentatomids in which we have been able to trace the courses of the tracheæ of the wings, the wing-veins are comparatively inconspicuous. We figure on this account one of the Coriidæ (*Hormostes reflexulus*) of which we have a specimen in which the tracheæ are distinctly visible within the well-developed veins (Fig. 23).

At the base of the wing the costa is remote from the costal edge of the wing, but approaches it near the middle of the thickened portion. The subcosta and radius coalesce to a point beyond the middle of this part of the wing, where the radial sector separates, making its characteristic curve. Vein R_1 is wanting. Media, cubitus, and the first anal vein extend in nearly direct lines to the membrane.

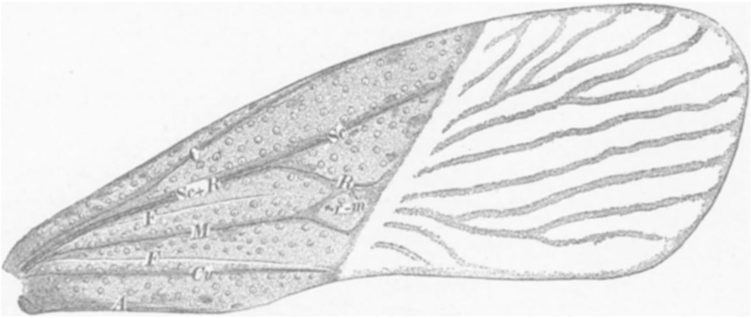

FIG. 23. — A Coreid, fore wing, adult.

The most important feature of the venation is the coalescence of subcosta and radius, a feature that occurs in many families of Hemiptera.

But the most important features to be observed are the positions of the furrows of the wing. Here the median furrow is in its typical position between radius and media. In the Pentatomids that we have studied it is more closely parallel with the radius and extends across the radial sector, showing that its position is not determined by the course of the veins. The anal furrow is in front of the cubitus instead of in its more usual position, behind this vein. In fact, in all of the Heteroptera that we have examined, when an anal furrow is distinctly developed it is in front of the cubitus.

Much remains to be done in tracing out the homologies of the wing-veins of the Hemiptera. But we feel that a good beginning has been made, one which will serve as a sure basis for future studies.

VI. THE VENATION OF THE WINGS OF LEPIDOPTERA.

In the order Lepidoptera the primitive type of wing venation is well preserved in certain of the Jugatæ. This is shown in Sthenopis (Fig. 24). In the species figured here, the deviations from our hypothetical type are few. In the fore wing, veins M_4 and Cu_1 coalesce for the greater part of their length, and one of the anal veins has been lost. In the hind wing, veins M_4 and Cu_1 anastomose, but separate near the margin of the wing.[1]

In the Frenatæ we find the primitive type well preserved in the fore wings of the more generalized forms. The most striking departure from our hypothetical type is the fact that the media is never more than three-branched;[2] and this is true also of the media of the hind wings. The wings of Prionoxystus

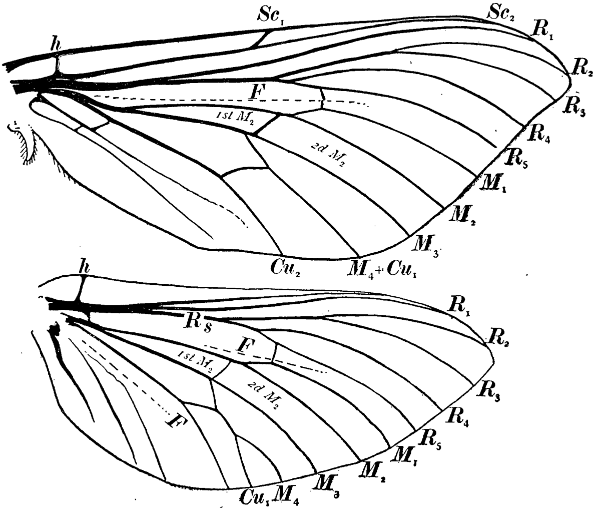

FIG. 24. — Wings of Sthenopis.

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[1] This is not true of the genus as a whole; usually these veins coalesce in the hind wings as in the fore wings.

[2] With our present knowledge it is impossible to determine the way that vein M_4 has disappeared in the Frenatæ. We have seen no indication that it coalesces with vein Cu_1 as in Sthenopis, for in all pupæ of this suborder that we have examined the medial trachea is only three-branched. We are obliged, therefore, to omit any further reference to this vein in the discussion of this order.

(Fig. 25) will serve to illustrate the type of venation characteristic of this suborder.

In the fore wing the branches of radius appear to present a complicated arrangement, but this is merely due to the anastomosis of veins R_3 and R_4; except for this the radial sector has preserved its primitive type. In this wing the bases of veins M_2 and M_3 have migrated towards the cubitus, so that cells 1st M_2 and 2d M_2 are not opposite each other (cell 1st M_2 is the small triangular cell near the center of the wing).

In the hind wing a great reduction of the subcosto-radial area of the wing has taken place. This has been brought about in two ways: first, veins Sc and R_1 coalesce from the margin of the wing nearly to the base of R_1;[1] and second, the radial sector is reduced to a single vein, R_s.

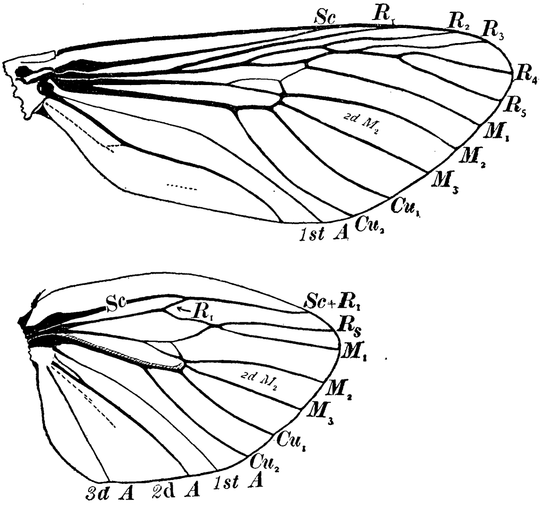

FIG. 25.—Wings of a Prionoxystus.

We have space to point out only one, the most important, of the ways in which this type is modified in the Frenatæ. It will be observed that the basal half of the wing, being traversed by the main stems of all of the veins, is stiffened to a great extent. Evidently, from what has taken place in the more specialized families, there is more vein-material here than is necessary or perhaps desirable, for we find a very general tendency towards the atrophy of the base of the media.

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[1] In pupæ of Frenatæ the subcostal trachea and the first branch of the radial trachea are distinct. This fact was first pointed out by Spuler.

An excellent record of what has taken place is preserved in the fore wing of the adult of Anosia (Fig. 26). Here the base of the media has disappeared, but there remain three little spurs projecting back into cell $R+M$ (indicated by the arrows) which show the positions occupied by the three branches of the media when the base of this vein ceased to be of use. It should be observed that in the pupa of this butterfly the medial trachea is well preserved throughout its entire length; the atrophy of the base of the media pertains only to the adult state.[1]

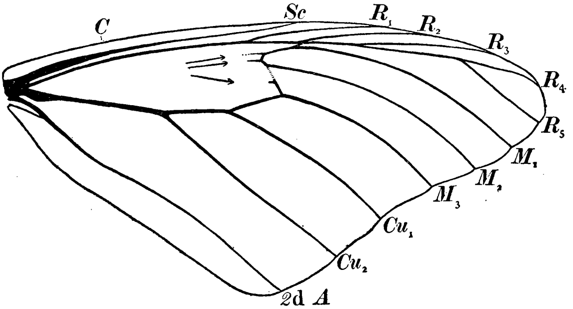

FIG. 26. — Fore wing of Anosia.

Correlated with the atrophy of the base of the media, there arises a necessity for a new source of air supply for the medial area of the distal half of the wing of the adult, and probably also for a better bracing of this part of the wing than would exist if no other changes were made. These are furnished by a more intimate connection of the branches of the media with the adjacent veins, vein M_1 becoming more intimately connected with the radial sector, vein M_3 with cubitus-one, and vein M_2 with one or the other of these veins, differing in different families.

There result from the changes just pointed out striking modifications of the courses of the veins concerned. Note, for example, that the base of vein M_3 in Anosia (Fig. 26) has migrated away from the spur indicating its more primitive position, and that the medio-cubital cross-vein (*m-cu*) is no longer transverse, but appears to be a continuation of the main stem of the cubitus.

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[1] Figures of the wings of pupæ of Lepidoptera are omitted, as several have been published by Spuler and others.

VII. THE VENATION OF THE WINGS OF TRICHOPTERA.

In the preceding pages much evidence has been given to show the importance of studying the tracheæ that precede the wing-veins, in order to determine with certainty the homologies of the latter. But in some of the orders of insects a remarkable reduction of the wing tracheæ has taken place, which renders them useless for this purpose. This is true of the Trichoptera and Diptera, and also to a considerable extent of the Hymenoptera.

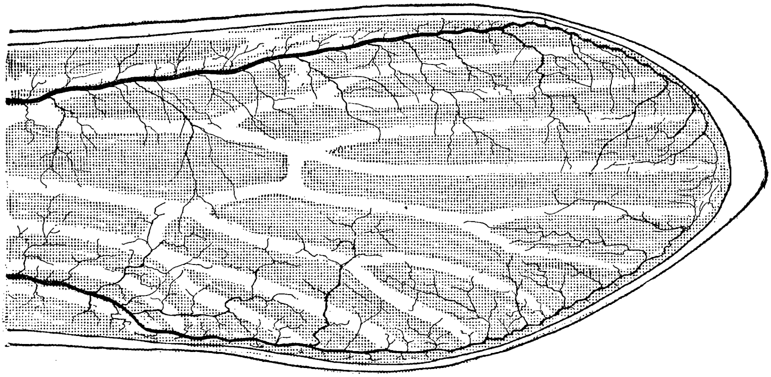

FIG. 27. — Wing of a pupa of a caddice fly.

If the wing of a pupa of a caddice fly be examined at that stage when the forming wing-veins appear as pale bands, it will be seen that the tracheation of the wing bears but little relation to the wing-veins. Usually only two or three main tracheæ are present; and although these may coincide with forming veins, their branches bear no relation whatever to veins (Fig. 27).

Fortunately, in the case of the Trichoptera we do not need to study tracheæ in order to determine the homologies of the wing-veins; for here, in the more generalized members of the order, we find the primitive type of wing venation well preserved.

The fore wing of Hydropsyche (Fig. 28) with a slight modification would serve as a typical insect wing. Excepting the coalescence of anal veins at the tip, the number and arrangement of the longitudinal veins in this wing correspond exactly with our hypothetical type; and only those cross-veins are present that may be considered typical on account of the frequency with which they occur in the more generalized members of different orders.

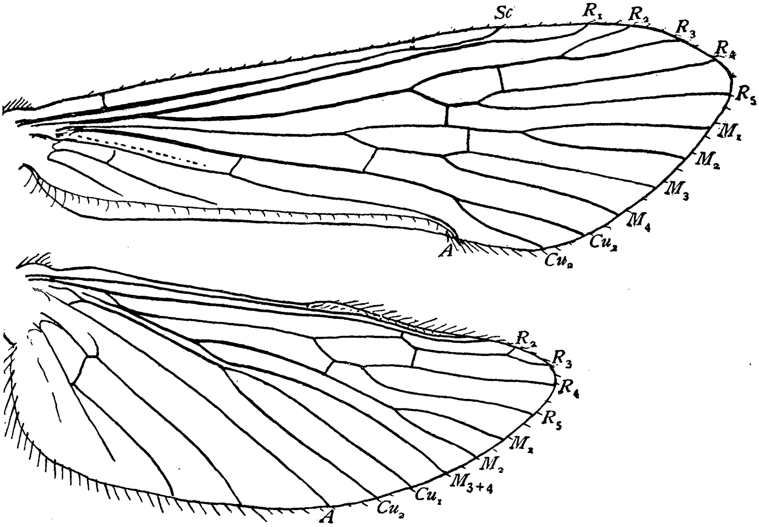

FIG. 28. — Wings of Hydropsyche.

In the hind wing the media is only three-branched and a tendency towards an increase in the number of anal veins is evident. This expansion of the anal area of the hind wings has been carried to a considerable extent in certain members of the order.

Lack of space prevents a discussion of the various ways in which the primitive type of wing venation is modified within this order. But such a discussion is hardly necessary, for it is not difficult to understand the venation of the wings of these insects.

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